

# North American Grouse: Issues and Strategies for the 21st Century

**Clait E. Braun**

Colorado Division of Wildlife  
Research Center  
Fort Collins

**Kathy Martin**

Canadian Wildlife Service and  
Department of Forest Sciences  
University of British Columbia  
Vancouver

**Thomas E. Remington**

Colorado Division of Wildlife  
Research Center  
Fort Collins

**Jessica R. Young**

Department of Biological Sciences  
Purdue University  
West Lafayette, Indiana

## Introduction

The 10 species of grouse (subfamily Tetraoninae) in North America occupy habitat types that vary from prairie, coniferous and deciduous woodlands, to alpine and arctic tundra. Prior to European settlement, grouse occurred in 47 of 49 continental states and all Canadian provinces (Aldrich 1963, Johnsgard 1973). While some species of grouse have been extirpated from many states and several provinces (especially prairie grouse species), grouse still occur in 46 of 49 continental states and all Canadian provinces.

Grouse have been hunted historically and, because of unique breeding displays, many species have been avidly pursued by photographers and bird watchers. The popularity of grouse has resulted in considerable attention by wildlife managers and researchers. Interest in hunting and conserving grouse was the impetus for the formation of one national private organization (The Ruffed Grouse Society) and several state organizations.

In this paper we give a brief review of the current status of grouse, identify issues that will confront managers in the future and identify strategies to resolve management dilemmas. We will argue for accelerating the evolution of the grouse management paradigm because we now are in serious danger of losing populations, subspecies and even species of grouse.

## Current Status of Grouse

### Prairie Grouse

This group includes the prairie-chickens/sh *T. pallidicinctus*, *T. phasianellus*) and sage Distribution and status of greater prairie-ch were enhanced (Aldrich 1963, Hamerstrom probably because cropland created dependabl Robb 1993). Because of intensification of extirpated from most of their acquired and p Manitoba, Saskatchewan, Iowa, Indiana, Oh One race now is extinct (heath hen) and ar (Attwater's). Populations are precarious in N North Dakota, Colorado, Missouri and Tex; in only four states (South Dakota, Nebraska

Lesser prairie-chickens historically occur *filifolia*) and shinnery oak (*Quercus havardii* (Aldrich 1963). While they still occur in a range, their distribution has decreased by habitat loss and deterioration (Taylor and Gut by an estimated 97 percent (Crawford 1980

Sharp-tailed grouse still occupy much of species (*T. p. columbianus*) has been extirpa (Giesen and Connelly 1993), and exists as percent of its former range (Miller and Gra as potentially threatened (category 2) by th Department of Interior 1989) under the Enc tailed grouse (*T. p. jamesi*) has been extirp Kansas, and there are < 200 individuals in t sharp-tailed grouse are undergoing range periphery of their range.

Sage grouse have been extirpated from t lumbia, New Mexico, Oklahoma, Nebraska abundance within their former core range ( currently occur in only 15 of 27 formerly o counties they persist as isolated remnants (t

Reductions in distribution and apparent a changes in land use, including increased c domestic livestock, conversion of shrublar maining habitats frequently are fragmented version, transportation systems, powerline development. Plant succession due to fire : useful for prairie grouse and serves as an i

### Forest Grouse

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## Current Status of Grouse

### Prairie Grouse

This group includes the prairie-chickens/sharp-tailed grouse (*Tympanuchus cupido*, *T. pallidicinctus*, *T. phasianellus*) and sage grouse (*Centrocercus urophasianus*). Distribution and status of greater prairie-chickens and sharp-tailed grouse initially were enhanced (Aldrich 1963, Hamerstrom and Hamerstrom 1963) by settlement, probably because cropland created dependable sources of winter food (Schroeder and Robb 1993). Because of intensification of land use, greater prairie-chickens were extirpated from most of their acquired and presumed core ranges (Alberta, Ontario, Manitoba, Saskatchewan, Iowa, Indiana, Ohio, Kentucky, Tennessee and Arkansas). One race now is extinct (heath hen) and another is federally listed as endangered (Attwater's). Populations are precarious in Michigan, Illinois, Minnesota, Wisconsin, North Dakota, Colorado, Missouri and Texas and secure enough to permit hunting in only four states (South Dakota, Nebraska, Oklahoma and Kansas).

Lesser prairie-chickens historically occupied suitable sand sagebrush (*Artemisia filifolia*) and shinnery oak (*Quercus havardii*) rangelands of the southern Great Plains (Aldrich 1963). While they still occur in all five states of their presumed original range, their distribution has decreased by 92 percent since the 1800s because of habitat loss and deterioration (Taylor and Guthery 1980), and numbers have decreased by an estimated 97 percent (Crawford 1980).

Sharp-tailed grouse still occupy much of their historic range. However, one subspecies (*T. p. columbianus*) has been extirpated from Oregon, Nevada and California (Giesen and Connelly 1993), and exists as isolated populations inhabiting < 10–50 percent of its former range (Miller and Graul 1980). This race has been designated as potentially threatened (category 2) by the U.S. Fish and Wildlife Service (U.S. Department of Interior 1989) under the Endangered Species Act. The plains sharp-tailed grouse (*T. p. jamesi*) has been extirpated from New Mexico, Oklahoma and Kansas, and there are < 200 individuals in Colorado (Hoag and Braun 1990). Thus, sharp-tailed grouse are undergoing range restriction at the western and southern periphery of their range.

Sage grouse have been extirpated from the periphery of their range (British Columbia, New Mexico, Oklahoma, Nebraska) and greatly reduced in distribution and abundance within their former core range (Braun 1987). For example, sage grouse currently occur in only 15 of 27 formerly occupied counties in Colorado; in several counties they persist as isolated remnants (C. E. Braun unpublished data).

Reductions in distribution and apparent abundance of prairie grouse are linked to changes in land use, including increased cultivation of land for crops, grazing by domestic livestock, conversion of shrublands to grasslands, and urbanization. Remaining habitats frequently are fragmented and smaller in size because of land conversion, transportation systems, powerline corridors, and reservoir and community development. Plant succession due to fire suppression has made some habitats less useful for prairie grouse and serves as an isolating mechanism.

### Forest Grouse

Three species of forest grouse occur in North America. Ruffed grouse (*Bonasa umbellus*) have the broadest distribution, spruce grouse (*Dendragapus canadensis*)

the most northern distribution, while blue grouse (*D. obscurus*) are restricted to the western United States and Canada (Aldrich 1963, Johnsgard 1973). The distribution of ruffed grouse decreased with settlement and clearing of forests; today its distribution has increased because of reversion of cropland to forests, reintroductions into historic range and introductions into new habitats (Newfoundland, Nevada and North Dakota) (reviewed in Gullion 1984, Widner et al. 1988).

The distribution of spruce grouse has changed little in the latter part of the 20th century other than significant retraction and fragmentation along the southern periphery of its range in northcentral and northwestern United States (Boag and Schroeder 1992). However, forest management that emphasizes large clear cuts and single species plantations has potential to negatively impact spruce grouse populations and distribution (Boag and Schroeder 1992). The greatest threats are in the boreal forest region of Canada, Alaska and in the northeastern United States. Depending on the size of areas cut, length of cutting cycles and forest regeneration rates, spruce grouse populations may remain depressed in local areas well into the 21st century under current forest management practices.

Blue grouse are residents of montane forests in western North America and generally occupy their known historic distribution. Some local extinctions such as at Mt. Pinos in California and reductions in distribution have occurred, probably the result of human activities (Bendell and Zwicker 1984, Zwicker 1992).

### *Ptarmigan*

Three species of ptarmigan occur in North America, although only the white-tailed ptarmigan (*Lagopus leucurus*) occurs south of the Canadian border (Aldrich 1963). This species has the most limited distribution of ptarmigan in North America, mostly the result of limited and irregular distribution of alpine habitats. White-tailed ptarmigan have been reintroduced into New Mexico, and transplanted successfully into non-native alpine ranges in California. Utah and Pikes Peak in Colorado (Braun et al. 1993). Although no significant range retraction has occurred, expansion of ski areas, roads and water developments have had local impacts on white-tailed ptarmigan, especially in the southern Rocky Mountains (Braun et al. 1976).

Both rock (*L. mutus*) and willow (*L. lagopus*) ptarmigan have circumpolar distributions in the northern hemisphere (Johnsgard 1983). In North America, both species occur across northern Canada and throughout most of Alaska (Aldrich 1963, Johnsgard 1983). While studies on changes in distribution and status of northern ptarmigan are lacking, it generally is believed their overall habitat has changed little in the last 30 years. However, mineral and oil extraction, fire, and increased human activities may have impacted rock and willow ptarmigan populations in local areas.

### **Current Policy**

Grouse management, research and harvest regulations have been the responsibility of state and provincial wildlife agencies without significant federal guidance. Federal funding has sponsored grouse research and management through the Pittman-Robertson Act, the National Science Foundation (U.S.), or the Natural Sciences and Engineering Research Council (Canada). However, federal land-management agen-

cies have been reluctant to alter management policies that conflict with commodity uses such as livestock grazing.

While state or provincial policies on grouse management have varied, past policies generally have focused on managing for abundant and widely distributed species and on protecting rare and endangered species. Ruffed grouse exist in the Upper Midwest Region (Minnesota, Wisconsin, Michigan, Pennsylvania) and in the United States, and all states have laws to maintain a diversity of seral stages on forested lands (Gullion 1984). Also, timber cutting rotations included in Forest Plans on numerous National Forests have contributed nearly \$2 million for research to test and improve management for ruffed grouse in the last 20 years.

Preservation of species is a policy of all states. Considerable attention has been given to the management of grouse populations at risk including hunting, a shift in responsibility from hunting to conservation, and endangered programs, local research effort and reintroductions into formerly occupied ranges.

This policy of emphasizing both abundant and rare species ignored species and subspecies. Lack of proactivity greatly restricts management options more costly and increases risk of extinction. Bureaucratic inertia of agencies also has contributed to a tendency to emphasize recovery efforts or involvement of other land-management agencies. Management efforts should reflect habitat potential and political boundaries. Emphasis has been on state and federal actions, not on the fate of local populations or global populations. Results in local extinctions and significant range retraction.

### **Perspectives for the 21st Century**

#### *Vision*

Steady increases in human populations with urbanization, mining, logging, roads and other development will reduce grouse habitats. Number of grouse will decline. Demand for viewing grouse and ecotourism will increase markedly. Single-species management to enhance grouse populations will be in favor of ecosystem management and preservation. Increasingly will be made in the glare of public interest and interested parties.

#### *Policy*

Grouse management policy should evolve to reflect changing conditions and management experiments that transcend

cies have been reluctant to alter management practices to favor grouse when alteration conflicts with commodity uses such as livestock grazing, logging and mining.

While state or provincial policies on grouse management have not been explicitly stated, past policies generally have focused on two extremes: enhancement of habitat to benefit abundant and widely distributed species to improve hunting, and preservation of rare and endangered species. Ruffed grouse exemplify the first approach. The Great Lakes Region (Minnesota, Wisconsin, Michigan, Pennsylvania) is the core of ruffed grouse range in the United States, and all states have active habitat manipulation programs to maintain a diversity of seral stages on forested land to increase ruffed grouse populations (Gullion 1984). Also, timber cutting rotations designed to benefit ruffed grouse are included in Forest Plans on numerous National Forests. The Ruffed Grouse Society has contributed nearly \$2 million for research to test the efficacy of this habitat development and improvement for ruffed grouse in the last 20 years.

Preservation of species is a policy of all management agencies, consequently, considerable attention has been given to threatened and endangered grouse. The amount of attention usually is correlated to the risk of extirpation. Typical agency responses to grouse populations at risk include: protection from or restrictions on hunting, a shift in responsibility from hunting programs within agencies to threatened and endangered programs, local research efforts, habitat acquisition and/or restoration, and reintroductions into formerly occupied range.

This policy of emphasizing both abundant hunted species and preserving endangered species ignored species and subspecies until they became endangered. This lack of proactivity greatly restricts management options, makes recovery of populations more costly and increases risk of extinction (Jennings and Scott 1993). Parochialism of agencies also has contributed to loss of populations of grouse. There is a tendency to emphasize recovery efforts on agency owned land and to minimize involvement of other land-management agencies and private interest groups. Management efforts should reflect habitat potential and not land ownership status or political boundaries. Emphasis has been on status of a species within the state, and not on the fate of local populations or global distribution. Benign neglect of local populations results in local extinctions and significant range retractions.

## **Perspectives for the 21st Century**

### *Vision*

Steady increases in human populations will result in even more land conversion, urbanization, mining, logging, roads and other developments which will further fragment and reduce grouse habitats. Number of grouse hunters will continue to decline. Demand for viewing grouse and ecotourism associated with grouse will increase markedly. Single-species management to enhance hunted populations will decline in favor of ecosystem management and preservation. Management decisions increasingly will be made in the glare of public scrutiny amid conflicting demands by interested parties.

### *Policy*

Grouse management policy should evolve to include landscape-level considerations and management experiments that transcend agency and political boundaries. This

will require unparalleled cooperation among management agencies and more and better research. Policy goals need to be defined for populations, subspecies and species of grouse. This will require the wisdom of Solomon, because a goal of preserving all local populations is unlikely to be feasible or even desirable in the broader context of managing for natural ecosystems and public needs and values. At the least, management should maintain current levels of grouse genetic variability and diversity at appropriate geopolitical scales, maintain biotic processes (speciation, population regulation, cycles, predator/prey relationships), retain suitable habitats to promote natural behaviors (i.e., lekking, migration patterns), and retain existing and evolving uses of grouse, such as hunting, viewing, education and ecotourism. Grouse management that achieves these goals will entail management of the places grouse live. Land management should be developed that allows grouse to be retained as components of functioning ecosystems.

### *Landscape and Life History Considerations*

Grouse evolved in large biomes and continuous landscapes. Prairie grouse (except sharp-tailed grouse) in most areas live in climax vegetation (grass prairies, sagebrush rangelands) and do not depend on disturbance to create habitat. Several forest grouse (ruffed grouse, coastal races of blue grouse) depend on fine-grained (stand level) fragmentation, such as early stages created by wind- or fire-induced gaps in mature forests. Interior races of blue grouse breed primarily in sagebrush/aspen habitat and winter in conifer stands. Thus, they depend on patchy, coarse-grained landscapes of open shrublands, and deciduous and coniferous forest. Prairie-chickens and sharp-tailed grouse followed the plows west and north during settlement and greatly expanded their original distributions. Coarse-grained fragmentation (addition of agriculture to prairies) was beneficial (providing a dependable winter food source) until prairie remnants became too small and isolated. Crawford and Bolen (1976) estimated that areas with less than 63 percent rangeland cannot support stable populations of lesser prairie-chickens.

The process of fragmentation caused by agriculture, forestry or urbanization creates heterogeneity and discontinuity at the landscape level. This is an issue of increasing urgency. The impact of fragmentation for wildlife species varies, with some highly vulnerable to landscape change and others more resilient. The sharpness of the "edges" between habitat patches and the surrounding "non-habitat" determines the extent to which fragmentation impacts bird populations, as does patch size, distance between patches and species life history characteristics (Rolstad 1991, Swenson and Angelstam 1993). For instance, fragmentation caused by regenerating clearcuts within forests impacts forest interior birds less than fragmentation caused by similar-sized cropped fields (Rolstad 1991).

Little research on grouse has been conducted at the landscape scale in North America with the exception of Fritz (1979). Grouse may be relatively intolerant to extensive fragmentation for several reasons related to their life history, namely specialized food habits, generalized anti-predator strategies and poor dispersal abilities. Grouse are specialized herbivores that tend to subsist on large amounts of low-quality forage (Martin et al. 1993). Several species have significantly different winter and summer diets. Thus, for many grouse, removal of forest or prairie equates directly to removing their food supply.

Grouse, their nests and young provide food predators. Grouse usually comprise a small, but a prey biomass in many of the communities they comprise only about 2 percent of the prey biomass (K. Martin unpublished data). Grouse clutches (21-27 days) in ground nests. Thus, in tundra, forest a significant item in the diet of egg predators for emergence of the young of other small- to medium-sized predators. Generalized anti-predator strategies proposed generalized anti-predator strategies such as camouflage. Generalized anti-predator strategies provide a small proportion of the prey biomass in the short-term increases in predators or reduced biomass impact grouse populations (Angelstam 1979, Storaa 1990). Coarse-grained fragmentation can result by exposing grouse to new predators. Finally, the habitat structure in forest or prairie also makes it easier for predators to locate eggs and young. Incidence of extinction in patches (Andren et al. 1985, Angelstam 1989, Wegge et al. 1990).

Extensive coarse-grained fragmentation can result in regional populations persist as local subpopulations. New York, Fritz (1979) found that spruce grouse within a larger deciduous forest was 95 percent of the area, 60 percent for smaller patches and 10 percent for kilometers of a colonization source. Rolstad (1991) found that 100 hectares were necessary for persistence of capercaillie. Presumably, populations in somewhat smaller patches or other subpopulations or core areas for recolonization.

Juvenile dispersal ability is a key variable in determining the viability of subpopulations as well as size and quality of patches (Rolstad 1991). Models incorporating dispersal ability were developed to predict competition (Carroll 1989). Recently, Hansen et al. (1993) developed models to incorporate different patch sizes, thus providing a means for poor colonizers with relatively short dispersal distances recorded for grouse range from 1 to 40 kilometers for females and 2 kilometers for males. Models should focus on the most philopatric sex (usually males) and on the most philopatric sex (usually males) of recolonizing patches based on dispersal ability. It appears likely that patch recolonization and viability are much reduced if fragments are more than 6 kilometers apart for grouse. However, dispersal distances measured in the field reflect the dispersal potential between habitats.

### *Issues and Strategies*

Extinction of populations of grouse due to

Grouse, their nests and young provide food for a suite of avian and mammalian predators. Grouse usually comprise a small, but seasonally significant proportion of the prey biomass in many of the communities they inhabit. For example, spruce grouse comprise only about 2 percent of the prey biomass in the boreal forests of the Yukon (K. Martin unpublished data). Grouse clutches contain large eggs that develop slowly (21–27 days) in ground nests. Thus, in tundra, forest and prairie, grouse eggs may comprise a significant item in the diet of egg predators for a period of 6–8 weeks prior to the emergence of the young of other small- to medium-sized prey species. Since grouse are not capable of defending their eggs and offspring from most predators, they have developed generalized anti-predator strategies such as cryptic coloration and behavior to evade predators. Generalized anti-predator strategies probably work best when grouse comprise a small proportion of the prey biomass in the communities they inhabit. However, short-term increases in predators or reduced biomass of alternate prey can negatively impact grouse populations (Angelstam 1979, Storaas and Wegge 1987, Wegge and Storaas 1990). Coarse-grained fragmentation can alter the predator/prey balance permanently by exposing grouse to new predators. Fine-grained changes such as simplifying the habitat structure in forest or prairie also may increase predation risk because it is easier for predators to locate eggs and young. Increased predation likely elevates the risk of extinction in patches (Andren et al. 1985, Andren and Angelstam 1988, Gjerde and Wegge 1989, Wegge et al. 1990).

Extensive coarse-grained fragmentation can lead to metapopulations, where regional populations persist as local subpopulations. In the Adirondack Mountains of New York, Fritz (1979) found that spruce grouse occupancy of coniferous patches within a larger deciduous forest was 95 percent if patches were larger than 100 hectares, 60 percent for smaller patches and 92 percent if patches were within 10 kilometers of a colonization source. Rolstad and Wegge (1987) determined 100 hectares were necessary for persistence of capercaillie (*Tetrao urogallus*) populations. Presumably, populations in somewhat smaller patches will persist if close enough to other subpopulations or core areas for recolonization.

Juvenile dispersal ability is a key variable that interacts with distance between subpopulations as well as size and quality of patches in determining metapopulation viability (Rolstad 1991). Models incorporating dispersal abilities of vertebrates initially were developed to predict competition for space (Murray 1967, Miller and Carroll 1989). Recently, Hansen et al. (1993) extended these dispersal ability models to incorporate different patch sizes, thus providing a conservation context. Grouse are poor colonizers with relatively short dispersal distances. The natal dispersal distances recorded for grouse range from 1 to 40 kilometers, with a median of about 5 kilometers for females and 2 kilometers for males (Table 1). Furthermore, managers should focus on the most philopatric sex (usually males) when calculating probabilities of recolonizing patches based on dispersal distances. For North American grouse, it appears likely that patch recolonization and significant genetic exchange will be much reduced if fragments are more than 6 kilometers apart, especially for forest grouse. However, dispersal distances measured in contiguous habitat may not accurately reflect the dispersal potential between habitat patches in fragmented landscapes.

### *Issues and Strategies*

Extinction of populations of grouse due to habitat loss, fragmentation, and degra-

Table 1. Mean natal dispersal for North American grouse.

Species	Location	Dispersal distance (km)		Habitat	Reference
		Females	Males		
Spruce grouse	Ontario	<1	<1	Boreal forest	Beaudette and Keppie 1992
Ruffed grouse	Wisconsin	4.8	2.1	Deciduous forest	Small and Rusch 1989
Blue grouse	British Columbia	2.0	1.1	Coastal conifer	Jamieson and Zwickel 1983
Greater prairie-chicken	Colorado	9.2	2.7	Sandhills/grain	Schroeder and Braun 1993
Sage grouse	Colorado	8.8	7.4	Sagebrush	Dunn and Braun 1985
White-tailed ptarmigan	Colorado	4.0	1.2	Alpine	Giesen and Braun 1993

dation is, and will continue to be, the most significant issue confronting grouse managers. Species most at risk are sage grouse, several races of greater prairie-chicken and sharp-tailed grouse, lesser prairie-chicken, and spruce grouse. Policy goals must be defined for populations, subspecies and species of grouse across political and agency boundaries. Working groups should be formed with representation by state and provincial wildlife agencies, federal land-management agencies, universities, conservation groups, private landowner groups and other interested parties to identify needs, acquire information, and develop plans for habitat restoration, acquisition and reintroductions of grouse. There are several recent examples of this approach in conservation. The North American Waterfowl Management Plan strives for integrated management of wetland ecosystems on public and private lands through partnerships among federal, state, provincial, territorial and tribal governments, private conservation organizations, and individuals (Nelson et al. 1991). The Interagency Scientific Committee formed in 1989 to coordinate U.S. Forest Service, U.S. Bureau of Land Management, U.S. Fish and Wildlife Service and National Park Service plans for managing the spotted owl (*Strix occidentalis*) was a landmark in the application of population viability analysis in conservation (Harrison et al. 1993). The prompt legal challenges by conservation groups and rejection of the Committee's strategy by a federal judge suggested that management plans should be developed before species reach critical levels, and conservation groups should be included in planning and analysis from the outset. It is time to form such partnerships for sage grouse, Columbian sharp-tailed grouse, Attwater's prairie-chicken and southern populations of spruce grouse.

Restoration of grouse populations will require reintroductions in addition to habitat management. Techniques for successful reintroductions have been developed for ruffed grouse (Gullion 1984), white-tailed ptarmigan (Hoffman and Giesen 1983), greater prairie-chicken (Hoffman et al. 1992) and sage grouse (Musil et al. 1993) and are being developed for other species of prairie grouse (Toepfer et al. 1990, Rodgers 1992). These techniques need to be tested broadly across habitats and species. Several points need to be considered relative to reintroductions of prairie grouse. Augmentation of existing small populations to reduce inbreeding and genetic bottlenecks (sensu Lande 1988, Lacy 1993) may not work (Caro and Laurenson 1994), and may

do more harm than good with lekking species. Large numbers ( $\geq 100$  ?) of birds from areas release sites should be transplanted as extreme grouse reduce effective population size and numbers of individuals may succeed in the s populations with restricted genetic variation is reduced (Lande 1988, Lacy 1993). Lekking have suffered the greatest declines.

Hunting, as a possible contributing factor it will become more contentious as habitats be the near term, hunting itself will be challenged or compensatory to natural mortality is debated (Bergerud 1988, Ellison 1991). Define that evaluate the extent to which hunting is a different patch sizes. Pending this information harvest regimes for small or fragmented populations the resilience of populations to hunting pressure.

To manage grouse populations effectively it is required. We need to know how much area and population processes, and how many inadequate genetic diversity. We need to know permit recolonization. How does habitat fragmentation processes? What levels of hunting are compensatory with fragmentation? We suspect that heavy game do not really understand the process. For most history data and habitat requirements for populations. Thus, we are in a good position to conduct some fine- and coarse-grained questions on fragmentation necessary to restore depleted habitats and, if seasonal habitats are critical. We must learn by implemented as experiments and evaluated (W

## Conclusions

We should be attempting to maintain growing habitats at both fine- and coarse-grain for management of grouse and their habitats and management must encompass local populations scales across agency and political boundaries of grouse populations. This will require habitat restoration, and better understanding populations and founders of new populations no longer will occur on the scale that it has increase. With enlightened habitat management American species of grouse can be expected. To expect less would indicate the public in environments in perpetuity.



do more harm than good with lekking species by reducing desirable or adaptive traits. Large numbers ( $\geq 100$  ?) of birds from areas as close and as similar as possible to release sites should be transplanted as extreme skews in mating success among lekking grouse reduce effective population size and restrict gene flow. Releases of small numbers of individuals may succeed in the short term, but the long-term ability of populations with restricted genetic variation to adapt to changes in local conditions is reduced (Lande 1988, Lacy 1993). Lekking grouse species are most at risk and have suffered the greatest declines.

Hunting, as a possible contributing factor in extinction of local grouse populations, will become more contentious as habitats become more fragmented and, at least in the near term, hunting itself will be challenged. The extent to which hunting is additive or compensatory to natural mortality is debatable for populations in continuous landscapes (Bergerud 1988, Ellison 1991). Definitive experiments need to be conducted that evaluate the extent to which hunting is additive at different harvest rates and in different patch sizes. Pending this information, agencies should adopt conservative harvest regimes for small or fragmented populations as fragmentation likely decreases the resilience of populations to hunting pressure.

To manage grouse populations effectively in the 21st century, additional knowledge is required. We need to know how much area is needed to maintain grouse populations and population processes, and how many individuals are necessary to maintain adequate genetic diversity. We need to know how close subpopulations should be to permit recolonization. How does habitat fragmentation and degradation impact population processes? What levels of hunting are compensatory or additive, and do these levels vary with fragmentation? We suspect that heavy grazing negatively impacts grouse, but we do not really understand the process. For most species of grouse, we have the basic life history data and habitat requirements for populations living in continuous landscapes. Thus, we are in a good position to conduct sophisticated experiments to address both fine- and course-grained questions on fragmentation. We do not have all the techniques necessary to restore depleted habitats and, for some grouse, we do not know which seasonal habitats are critical. We must learn by trying. Management strategies should be implemented as experiments and evaluated (Walters 1986).

## Conclusions

We should be attempting to maintain grouse populations and processes by managing habitats at both fine- and course-grained levels. To achieve this goal, policies for management of grouse and their habitats must change in the 21st century. Planning and management must encompass local populations but be implemented at landscape scales across agency and political boundaries. Increased emphasis is needed on restoration of grouse populations. This will require methodology for reintroductions and habitat restoration, and better understanding of the importance of genetics of small populations and founders of new populations. Hunting of many grouse populations no longer will occur on the scale that it has in the past, although other uses will increase. With enlightened habitat management and government policies, all North American species of grouse can be expected to persist throughout the 21st century. To expect less would indicate the public is not committed to maintaining quality environments in perpetuity.



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## References

- Aldrich, J. W. 1963. Geographic orientation of American Tetraonidae. *J. Wildl. Manage.* 27: 529-545.
- Angelstam, P. 1979. Black grouse *Lyrurus tetrix* reproductive success and survival rate in peak and crash small-rodent years in central Sweden. Pages 101-111 in T. W. I. Lovel, ed., *Woodland Grouse Symp.*, Inverness, Scotland. World Pheasant Assoc., Bures, U.K.
- Andren, H. and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: Experimental evidence. *Ecology* 69: 544-547.
- Andren, H., P. Angelstam, E. Lindstrom and P. Widen. 1985. Differences in predation pressure in relation to habitat fragmentation: An experiment. *Oikos* 45: 273-277.
- Beaudette, P. D. and D. M. Keppie. 1992. Survival of dispersing spruce grouse. *Can. J. Zool.* 70: 693-697.
- Bendall, J. F. and F. C. Zwickel. 1984. A survey of the biology, ecology, abundance, and distribution of the blue grouse (Genus *Dendragapus*). *Int. Grouse Symp.*, World Pheasant Assoc., Suffolk, U.K. 3: 163-190.
- Bergerud, A. T. 1988. Increasing the numbers of grouse. Pages 686-731 in A. T. Bergerud and M. W. Gratson, eds., *Adaptive strategies and population ecology of northern grouse*. Univ. Minnesota Press, Minneapolis.
- Boag, D. A. and M. A. Schroeder. 1992. Spruce grouse. In A. Poole, P. Stettenheim and F. Gill, eds., *The Birds of North America*, No. 5. Philadelphia Acad. Nat. Sci. and Am. Ornith. Union, 28 pp.
- Braun, C. E. 1987. Current issues in sage grouse management. *Proc. West. Assoc. Fish and Wildl. Agencies* 67: 134-144.
- Braun, C. E., R. W. Hoffman and G. E. Rogers. 1976. Wintering areas and winter ecology of white-tailed ptarmigan in Colorado. *Spec. Rept.* 38. Colorado Div. Wildl., Denver. 38 pp.
- Braun, C. E., K. Martin and L. A. Robb. 1993. White-tailed ptarmigan. In A. Poole and F. Gill, eds., *The Birds of North America*, No. 68. Philadelphia Acad. Nat. Sci. and Am. Ornith. Union, 24 pp.
- Caro, T. M. and M. K. Laurenson. 1994. Ecological and genetic factors in conservation: A cautionary tale. *Science* 263: 485-486.
- Crawford, J. A. 1980. Status, problems and research needs of the lesser prairie chicken. Pages 1-7 in P. A. Vohs and F. L. Knopf, eds., *Proc. Prairie Grouse Symp.* Oklahoma St. Univ., Stillwater.
- Crawford, J. A. and E. G. Bolen. 1976. Effects of land use on lesser prairie-chickens in Texas. *J. Wildl. Manage.* 40: 96-104.
- Dunn, P. O. and C. E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. *Auk* 102: 621-627.
- Ellison, L. N. 1991. Shooting and compensatory mortality in tetraonids. *Ornis Scand.* 22: 229-240.
- Fritz, R. S. 1979. Consequences of insular population structure: Distribution and extinction of spruce grouse populations. *Oecologia* 42: 57-65.
- Giesen, K. M. and C. E. Braun. 1993. Natal dispersal and recruitment of juvenile white-tailed ptarmigan in Colorado. *J. Wildl. Manage.* 57: 72-77.
- Giesen, K. M. and J. W. Connelly. 1993. Guidelines for management of Columbian sharp-tailed grouse habitats. *Wildl. Soc. Bull.* 21: 325-333.
- Gjerde, I. and P. Wegge. 1989. Spacing pattern, habitat use and survival of capercaillie in a fragmented winter habitat. *Ornis Scand.* 20: 219-225.
- Gullion, G. W. 1984. Ruffed grouse management—Where do we stand in the eighties? Pages 169-181 in W. L. Robinson, ed., *Ruffed grouse management: State of the art in the early 1980's*. Book Crafters, Chelsea, MI.
- Hamerstrom, F. and F. Hamerstrom. 1963. The symposium in review. *J. Wildl. Manage.* 27: 869-887.
- Hansen, A. J., S. L. Garman, B. Marks and D. L. Urban. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. *Ecol. Applic.* 3: 481-496.
- Harrison, S., A. Stahl and D. Doak. 1993. Spatial mode issues behind recent events. *Conserv. Biol.* 7: 95.
- Hoag, A. W. and C. E. Braun. 1990. Status and distribution. *Prairie Nat.* 22: 97-102.
- Hoffman, R. W. and K. M. Giesen. 1983. Demography of ptarmigan. *Can. J. Zool.* 61: 1758-1764.
- Hoffman, R. W., W. D. Snyder, G. C. Miller and C. E. Braun. 1988. Status and distribution of prairie-chickens in northeastern Colorado. *Prairie Nat.* 20: 97-102.
- Jamieson, I. G. and F. C. Zwickel. 1983. Dispersal and survival. *Can. J. Zool.* 61: 570-573.
- Jennings, M. D. and J. M. Scott. 1993. Building a new biodiversity match reality? *Renewable Resour. J.*
- Johnsgard, P. A. 1973. Grouse and quails of North America. *Univ. Nebraska Press*, Lincoln.
- . 1983. *The grouse of the world*. Univ. Nebraska Press, Lincoln.
- Lacy, R. C. 1993. Impacts of inbreeding in natural and managed populations: Perspectives Biol. and Med. 36.
- Lande, R. 1988. Genetics and demography in biological conservation. *Evolution* 42: 981-990.
- Martin, K., R. F. Holt and D. W. Thomas. 1993. Grouse and alpine grouse. Pages 33-41 in C. Carey, G. I. Bawa, and J. H. Law, eds., *Life in the cold III: Ecological, physiological, and evolutionary aspects*. Boulder, CO.
- Miller, G. C. and W. D. Gaul. 1980. Status of sharp-shinned hawk. *Proc. Prairie Nat.* 22: 97-102.
- Miller, G. L. and B. W. Carroll. 1989. Modeling vertebrate distribution. *Ecology* 70: 977-986.
- Murray, B. G. J. 1967. Dispersal in vertebrates. *Ecol. Monogr.* 37: 1-47.
- Musil, D. D., J. W. Connelly and K. P. Reese. 1993. Grouse translocated to central Idaho. *J. Wildl. Manage.* 57: 72-77.
- Nelson, H. K., R. G. Streeter and J. D. McCuaig. 1991. Waterfowl Management Plan. *Trans. No. Am. Wildl. Nat. Hist.* 10: 1-10.
- Rodgers, R. D. 1992. A technique for establishing sharp-shinned hawk. *Soc. Bull.* 20: 101-106.
- Rolstad, J. 1991. Consequences of forest fragmentation: conceptual issues and the evidence. *Biol. J. Linnean Soc.* 43: 31-51.
- Rolstad, J. and P. Wegge. 1987. Distribution and survival of capercaillie. *Oecologia* 72: 389-394.
- Schroeder, M. A. and C. E. Braun. 1993. Partial migration in northeastern Colorado. *Auk* 110: 21-28.
- Schroeder, M. A. and L. A. Robb. 1993. Greater prairie-chicken. In A. Poole and F. Gill, eds., *The Birds of North America*, No. 36. Philadelphia Acad. Nat. Sci. and Am. Ornith. Union, 24 pp.
- Small, R. J. and D. H. Rusch. 1989. The natal dispersal of sharp-shinned hawk. *Proc. Prairie Nat.* 22: 97-102.
- Storaas, T. and P. Wegge. 1987. Nesting habitats of capercaillie and black grouse. *J. Wildl. Manage.* 51: 37-47.
- Swenson, J. E. and P. Angelstam. 1993. Habitat separation in relation to boreal forest succession. *Can. J. Zool.* 71: 100-104.
- Taylor, M. A. and F. S. Guthery. 1980. Status, ecology and management of sharp-shinned hawk. *U.S. Dept. Agric., For. Serv. Gen. Tech. Rept.* 147.
- Toepfer, J. E., R. L. Eng and R. K. Anderson. 1990. Endangered and threatened species. *Trans. No. Am. Wildl. and Natur. Res.* 10: 1-10.
- U.S. Department of the Interior. 1989. Endangered and threatened species. *Fed. Regist.* 54: 560.
- Walters, C. J. 1986. Adaptive management of renewable resources. *Conserv. Biol.* 1: 94-104.
- Wegge, P. and T. Storaas. 1990. Nest loss in capercaillie and black grouse in southeast Norway. *Oecologia* 84: 37-47.
- Wegge, P., I. Gjerde, L. Kastdalen, J. Rolstad and T. Storaas. 1993. The mortality rate of capercaillie? *Int. Union G.*

- Harrison, S., A. Stahl and D. Doak. 1993. Spatial models and spotted owls: Exploring some biological issues behind recent events. *Conserv. Biol.* 7: 950-953.
- Hoag, A. W. and C. E. Braun. 1990. Status and distribution of plains sharp-tailed grouse in Colorado. *Prairie Nat.* 22: 97-102.
- Hoffman, R. W. and K. M. Giesen. 1983. Demography of an introduced population of white-tailed ptarmigan. *Can. J. Zool.* 61: 1,758-1,764.
- Hoffman, R. W., W. D. Snyder, G. C. Miller and C. E. Braun. 1992. Reintroduction of greater prairie-chickens in northeastern Colorado. *Prairie Nat.* 24: 197-204.
- Jamieson, I. G. and F. C. Zwickel. 1983. Dispersal and site fidelity in blue grouse. *Can. J. Zool.* 61: 570-573.
- Jennings, M. D. and J. M. Scott. 1993. Building a macroscope: How well do places managed for biodiversity match reality? *Renewable Resour. J.* 11(2): 16-20.
- Johnsgard, P. A. 1973. Grouse and quails of North America. Univ. Nebraska Press, Lincoln. 553 pp.
- . 1983. The grouse of the world. Univ. Nebraska Press, Lincoln. 413 pp.
- Lacy, R. C. 1993. Impacts of inbreeding in natural and captive populations of vertebrates: Implications for conservation. *Perspectives Biol. and Med.* 36: 480-496.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241: 1,455-1,460.
- Martin, K., R. F. Holt and D. W. Thomas. 1993. Getting by on high: Ecological energetics of arctic and alpine grouse. Pages 33-41 in C. Carey, G. L. Florant, B. A. Wunder and B. Horwitz, eds., *Life in the cold III: Ecological, physiological, and molecular mechanisms*. Westview Press, Boulder, CO.
- Miller, G. C. and W. D. Gaul. 1980. Status of sharp-tailed grouse in North America. Pages 18-28 in P. A. Vohs and F. L. Knopf, eds., *Proc. Prairie Grouse Symp.* Oklahoma St. Univ., Stillwater.
- Miller, G. L. and B. W. Carroll. 1989. Modeling vertebrate dispersal distances: Alternatives to the geometric distribution. *Ecology* 70: 977-986.
- Murray, B. G. J. 1967. Dispersal in vertebrates. *Ecology* 48: 975-978.
- Musil, D. D., J. W. Connelly and K. P. Reese. 1993. Movements, survival, and reproduction of sage grouse translocated into central Idaho. *J. Wildl. Manage.* 57: 85-91.
- Nelson, H. K., R. G. Streeter and J. D. McCuaig. 1991. Accomplishments of the North American Waterfowl Management Plan. *Trans. No. Am. Wildl. and Natur. Resour. Conf.* 56: 439-452.
- Rodgers, R. D. 1992. A technique for establishing sharp-tailed grouse in unoccupied range. *Wildl. Soc. Bull.* 20: 101-106.
- Rolstad, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: Conceptual issues and the evidence. *Biol. J. Linnean Soc.* 42: 149-163.
- Rolstad, J. and P. Wegge. 1987. Distribution and size of capercaillie leks in relation to old forest fragmentation. *Oecologia* 72: 389-394.
- Schroeder, M. A. and C. E. Braun. 1993. Partial migration in a population of greater prairie-chickens in northeastern Colorado. *Auk* 110: 21-28.
- Schroeder, M. A. and L. A. Robb. 1993. Greater prairie-chicken. In A. Poole, P. Stettenheim and F. Gill, eds., *The birds of North America*, No. 36. Philadelphia Acad. Nat. Sci. and Am. Ornith. Union. 24 pp.
- Small, R. J. and D. H. Rusch. 1989. The natal dispersal of ruffed grouse. *Auk* 106: 72-79.
- Storaas, T. and P. Wegge. 1987. Nesting habitats and nest predation in sympatric populations of capercaillie and black grouse. *J. Wildl. Manage.* 51: 167-172.
- Swenson, J. E. and P. Angelstam. 1993. Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. *Can. J. Zool.* 71: 1,303-1,310.
- Taylor, M. A. and F. S. Guthery. 1980. Status, ecology and management of the lesser prairie chicken. U.S. Dept. Agric., For. Serv. Gen. Tech. Rept. RM-77. 15 pp.
- Toeffer, J. E., R. L. Eng and R. K. Anderson. 1990. Transplanting prairie grouse—What have we learned? *Trans. No. Am. Wildl. and Natur. Resour. Conf.* 55: 569-579.
- U.S. Department of the Interior. 1989. Endangered and threatened wildlife and plants; annual notice of review; proposed rules. *Fed. Regist.* 54: 560.
- Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan Co., New York, NY. 374 pp.
- Wegge, P. and T. Storaas. 1990. Nest loss in capercaillie and black grouse in relation to the small rodent cycle in southeast Norway. *Oecologia* 82: 527-530.
- Wegge, P., I. Gjerde, L. Kastdalen, J. Rolstad and T. Storaas. 1990. Does forest fragmentation increase the mortality rate of capercaillie? *Int. Union Game Biol.* 19: 448-453.

- Widner, M. R., D. A. James, K. G. Smith and M. E. Cartwright. 1988. Reintroduction, dispersal, and survivorship of ruffed grouse reintroduced into Arkansas. *Proc. Southeast. Assoc. Fish and Wildl. Agencies* 42: 349-357.
- Zwicker, F. C. 1992. Blue grouse. *In* A. Poole, P. Stettenheim and F. Gill, eds., *The Birds of North America*, No. 15. Philadelphia Acad. Nat. Sci. and Am. Ornith. Union. 28 pp.

## Population Status and Trends of Prairie-chickens from the Breeding Bird Survey and

**John R. Sauer**

*National Biological Survey  
Patuxent Wildlife Research Center  
Laurel, Maryland*

**Sandra Orsillo**

*National Biological Survey  
Patuxent Wildlife Research Center  
Laurel, Maryland*

**Bruce G. Peterjohn**

*National Biological Survey  
Division of Inventory and Monitoring  
Patuxent Wildlife Research Center  
Laurel, Maryland*

### Introduction

The North American Breeding Bird Survey and the Canadian Wildlife Biological Survey provide information on population change of American breeding birds. The Audubon Christmas Bird Count provides distribution data on populations of birds wintering in the United States. Game managers have been examining both the BBS and CBC for information on population status of upland game birds. For example, the BBS provides useful population data on the northern bobwhite (*Colinus virginianus*) and other quail.

In this paper, we assess the capabilities of the BBS to estimate population trends of grouse and prairie-chickens from the surveys, present the distribution of each species from the surveys, present the methodology for each species, conduct a power analysis on the BBS data in each survey for monitoring population trends of prairie-chickens. We conduct these analyses for blue grouse (*D. canadensis*), ruffed grouse (*Bonasa umbellus*), sharp-tailed grouse (*Tympanuchus phasianus*), sharp-tailed grouse (*Tympanuchus phasianus*), sharp-tailed grouse (*Tympanuchus phasianus*) and lesser prairie-chickens (*T. cupido*) and lesser prairie-chickens.

### Methods

#### *The North American Breeding Bird Survey*

The BBS (Peterjohn and Sauer 1993) is conducted primarily in June in the United States and southern Canada. The 3,000 survey routes consists of 50 stops spaced